



Research article

Morphological acclimation to agronomic manipulation in leaf dispersion and orientation to promote “Ideotype” breeding: Evidence from 3D visual modeling of “super” rice (*Oryza sativa* L.)



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ABSTRACT

Food security is confronted by major threats from crop yield stagnation and global climate change. The benefits of phenotypic plasticity across environments for given crop genotypes are thought to be imperative for high-yielding cropping systems. Given that 3D modeling is increasingly recognized for dissecting crop phenotypic plasticity, it requires an assessment of the potential benefits of architectural adaptation of super rice to different agronomic practices. In this study, we focused on a comprehensive evaluation of the phenotypic plasticity of super rice on the aspects of 3D architectural “reoptimization,” photosynthetic productivity, nitrogen economy, and grain yield. A super rice phenotype in superhigh-yielding practice (SH) displays a “reoptimized” morphogenesis in the leaf vertical dispersion and orientation in comparison to that in Farmer’s practice (FP). Specifically, a super rice phenotype in SH is provided with a high cumulative rate and peaks of leaf area, increasing the distribution of high leaf inclination angles in comparison to that in FP, particularly in the upper parts of the canopy. These “reoptimizations” sustained profits in light environment within a canopy, leaf area duration, photosynthetic light harvest, and light utilization efficiency and were coordinated with improving nitrogen uptake and assimilation. The current literature indicates that the agronomic plasticity of super rice in architectural “reoptimization” is a promising perspective for high yield formation. Our results suggest that more emphasis should be placed upon agronomic adaptation strategies for super rice across diverse genotypes and environments to further improve crop establishment and photosynthetic productivity.

1. Introduction

Globally, an increasing human population will increase global food demand (Godfray et al., 2010; Fahad et al., 2017). Climate change impacts from increasing temperature (Peng et al., 2004; Lobell et al., 2012, 2013; Fahad et al., 2016a,b,c,d; Fahad et al., 2018) and decreasing solar radiation (Wang et al., 2009) are further threats to agricultural productivity (Wheeler and von Braun, 2013). It is essential

to adopt sustainable and efficient intensification of agricultural practices (Tilman, 1999; Tilman et al., 2011; Fahad and Bano, 2012; Fahad et al., 2013; Fahad et al., 2014a,b; Fahad et al., 2015a,b; Wu et al., 2017; Yang et al., 2017; Noman et al., 2017; Saud et al., 2013; Saud et al., 2014; Saud et al., 2016; Saud et al., 2017) and envision new crop phenotypes for productive cropping systems (McKersie, 2015). Particularly, a study indicated that crop yield potential (Y_p) is reaching its biological ceiling (Zhu et al., 2010). The yield potential of a given

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Abbreviation

CGR	crop growth rate ($\text{g m}^{-2} \text{d}^{-1}$)
LAD	leaf area duration ($\text{m}^2 \text{d m}^{-2}$)
N_l	leaf nitrogen content per unit area of ground (g m^{-2})
N_{grain}	filled grain nitrogen content per unit area of ground (g m^{-2})
N_t	total aboveground nitrogen content per unit area of ground (g m^{-2})
N_{tr}	pre-anthesis nitrogen translocation per unit area of ground (g m^{-2})

Pre-Nt	pre-anthesis nitrogen content (g m^{-2})
Post-Nt	post-anthesis nitrogen content (g m^{-2})
S_i	the integral of intercepted solar radiation (MJ m^{-2})
SLN	nitrogen content per unit leaf area (g m^{-2})
SPAD	soil and plant analyzer development
S_t	the integral of incident solar radiation (MJ m^{-2})
ϵ_c	efficiency of conversion of intercepted radiation into dry matter (g MJ^{-1})
ϵ_i	efficiency of interception of solar radiation (%)
ϵ_p	harvest index (%)

genotype is the product of the integral of incident solar radiation per unit area of land (S_i), efficiency in the interception of solar radiation (ϵ_i), efficiency in the conversion of intercepted radiation into dry matter (ϵ_c), and harvest index (ϵ_p): $Y_p = S_i \epsilon_i \epsilon_c \epsilon_p$ (Long et al., 2015). Meanwhile, the ϵ_i and ϵ_p of two major food crops, rice and wheat, are now approaching plateaus (Parry et al., 2011; Long et al., 2015). With reference to this equation, ϵ_c primarily determined by photosynthesis has been considered an important prospect for improving Y_p (Long et al., 2015). There are many opportunities to increase total intercepted solar radiation (S_i) such as improving early vigor (Rebolledo et al., 2015) or introducing stay-green genotypes (Thomas and Ougham, 2014). Crop yield is strongly associated with the photosynthetic productivity of the crop (Ainsworth and Long, 2005).

Plant architecture significantly affects photosynthetic biochemistry and plant physiology and is a major factor in high-throughput phenotyping (Li et al., 2003; Sakamoto and Matsuoka, 2004). Green revolution goals feature reduced canopy height and efficient canopy architecture resulting in productive rice phenotypes with higher ϵ_p (Khush, 1996). A new cultivar of rice defined as an “Ideotype” displayed efficient canopy architecture and high photosynthetic productivity and grain production (Peng et al., 2008). Super rice combined the “Ideotype” canopy architecture and utilization of intersubspecific heterosis (Yuan, 2001) has resulted in great contributions to grain production in China (Cheng et al., 2007). Thus, identification of optimal canopy architecture features can expedite “Ideotype” breeding for higher crop productivity (Peng et al., 2008; Parry et al., 2011). Accurate physiological phenotyping of specific plant traits appears to be essential in developing high-yield cultivars (Ghanem et al., 2015). In combination, phenotypic “reoptimization” of super rice with morphological and agronomic manipulation could guarantee a higher yield potential.

Many researchers have concluded that plant architecture and topology are important characteristics for crop performance and agro-ecological adaptation and thus deserve systematic investigation using 3D architecture models (Rötter et al., 2015; Ramirez-Villegas et al., 2015; Christensen et al., 2018). The understanding of the roles of canopy architectural characteristics and phenotypic traits has relied extensively on qualitative and quantitative models from different perspectives. Literature shows research studies containing 3D digitizing for maize (Sinoquet et al., 1991); sorghum (Kaitaniemi et al., 1999); and beans, cotton, grapevine plants and oil palm (Room et al., 1996; Sinoquet et al., 1998; Perez et al., 2018). In addition, a few models representing 3D visual confirmation of canopy architectures for maize (Fournier and Andrieu, 1998; España et al., 1999; Guo et al., 2006; Chaivivatrakul et al., 2014), sorghum (Kaitaniemi et al., 2000), wheat (Fournier et al., 2003; Evers et al., 2007) and rice (Watanabe et al., 2005; Zheng et al., 2008; Sharma et al., 2013; Burgess et al., 2017) have been introduced in the agricultural field. Most were mathematical and geometrical analyses of an individual crop canopy and lacked comprehensive confirmations of leaf dispersion and orientation; light environment within a canopy; interaction of the nitrogen (N) economy and photosynthetic performance; and, in particular, high attainable economic yield.

Despite the availability of improved crop phenotypes with increased yield potential, the highest crop productivity has not been attained because of poor agricultural practices (Reynolds and Tuberosa, 2008). Meanwhile, laboratory examination of key plant architecture and topology may complement direct phenotyping in the field, but such traits do not always adapt well to field conditions (Araus and Cairns, 2014; Christensen et al., 2018). Constraints in phenotyping capability currently limit our abilities to dissect genetic information for the morphological and physiological traits of rice, particularly for those complex traits related to high-yield (Sharma et al., 2013). Thus, “Ideotype” rice phenotype breeding should be based on high-throughput phenotyping (e.g., super rice). Previously, studies of the morphogenesis of rice plant structures have been conducted under pot (Watanabe et al., 2005) and field conditions (Zheng et al., 2008; Burgess et al., 2017). However, a lack of a comprehensive evaluation of leaf dispersion and orientation, ϵ_i , ϵ_c , N economy, and yield in super rice based on 3D visual canopy architecture under high-yielding agro-ecological environments remains. It is urgently required to provide information for the development of productive genotypes and the design of high-yielding practices to optimize canopy architectures in competitive environments.

In the current study, we evaluated the 3D canopy architectural characteristics of super rice under a high-yielding agro-environment (SH, super high-yielding practice) in comparison to that under traditional agro-environments (FP, Farmer's practice) based on our previous annually high-yielding studies beginning in 2007. In our previous studies, we demonstrated that the grain yield of SH was near the climatic yield potential of the Middle Reaches of the Yangtze River (Wang et al., 2016a, 2016b). The objectives of the current research were i) to determine the plasticity of the canopy architecture of the super rice using 3D visual modeling; ii) evaluate the architectural and physiological characteristics that contribute to the higher productivity of super rice; and iii) calculate the correlation of photosynthetic productivity with plant morphology traits, light utilization, and N economy.

2. Materials and methods

2.1. Plant materials and experimental treatments

This study was simultaneously conducted with a study of the relative importance of temperature and radiation on the yield difference of double-season rice between tropical and subtropical environments (Wang et al., 2016a). The present study was conducted in the subtropical environment of Wuxue county ($29^{\circ}51'N$ $115^{\circ}33'E$, 51 m altitude), Hubei Province, China, during the late season from June to November 2012. Field experiments with super rice (*Oryza. sativa* L.) cultivar Tianyouhuazhan were arranged using four replicates. The experimental soil had the following properties in the upper 20 cm: pH of 5.1, 29.7 g kg^{-1} of organic matter, 2.7 g kg^{-1} of total N, 38.3 mg kg^{-1} of Olsen P, and 301.8 mg kg^{-1} of exchangeable K. There were two practices. FP and SH represented Farmer's practice and Super high-yielding, respectively. The plot size of the FP and SH treatments was 90.0 and 130.0 m^2 , respectively. SH proved to be competent for

maximizing the grain yield of a double-season rice crop in our subsequent studies (Wang et al., 2016b). Pregerminated seeds were sown in a seedbed on June 18, 2012.

The differences between FP and SH are summarized in Supplementary Table S1. For the FP treatment, N as ammonium bicarbonate was applied at basal while N as urea was applied at mid-tillering. P as superphosphate was applied at basal while K as KCl was applied at midtillering. For the SH treatment, we increased (1) the rates of N, P, and K application, (2) the times of N and K application, and (3) plant density with narrower hill spacing and more seedlings per hill compared with FP. High nutrient input was used to ensure that the yield potential of rice was not limited by nutrient supply. Specifically, basal N application was consist of 78.8 kg N ha⁻¹ as compound fertilizer and 53.8 kg N ha⁻¹ as ammonium bicarbonate. Urea was used for top-dressing in SH. Phosphorus was applied only at basal for SH with 34.4 kg P ha⁻¹ as compound fertilizer and 16.5 kg P ha⁻¹ as superphosphate. Potassium for SH was applied at basal, midtillering, and panicle initiation. At basal, 65.3 kg K ha⁻¹ as compound fertilizer was applied. Potassium chloride was used for K topdressing with 87.4 kg K ha⁻¹ at midtillering and 52.3 kg K ha⁻¹ at panicle initiation. Insects, diseases, and weeds were intensively controlled using chemicals to avoid yield loss.

2.2. Plant growth analyses and yield determination

Chlorophyll meter (SPAD-502, Minolta, Ramsey, NJ) readings were taken to determine the leaf SPAD value dynamic in all the plots during the regreening (1), midtillering (3), panicle initiation (4), anthesis (5),

and maturity stages (9). The equivalent of days after transplanting for the five stages was 14, 26, 33, 62 and 99, respectively. Twelve hills of rice were chosen at random in each plot, and three readings were taken at each hill from the uppermost fully expanded leaf. Stem number was measured every 3–4 days beginning 11 days after transplanting. During the panicle initiation and anthesis stages, 12 hills were chosen from each plot to measure the leaf area index (LAI) and aboveground dry matter (DM). At maturity, grain yield was determined from a 5-m² area in each plot and adjusted to the standard moisture content of 0.14 g H₂O g⁻¹ fresh weight. At the same time, 12 hills were diagonally taken from this 5-m² area in each plot in which grain yield was determined to measure the LAI and aboveground DM. Plants were separated into leaves, stems, and panicles. Grain moisture content was measured using a digital moisture tester (DMC-700, Seedbuco, Chicago, IL, USA). Green leaf area was measured using a leaf area meter (LI-3000, LI-COR Inc., Lincoln, NE, USA) expressed as LAI and leaf area duration (LAD).

$$\text{LAD (m}^2 \text{ d m}^{-2}) = 1/2 \times (L_1 + L_2) \times (t_2 - t_1) \quad (1)$$

L_1 and L_2 are the LAI (m² m⁻²) and t_1 and t_2 are the days after transplanting (d) according to Monsi and Saeki (2005). The DM of leaves, stems, and panicles was measured following oven drying at 80 °C to a constant weight. Crop growth rate (CGR, g m⁻² d⁻¹) was calculated as the ratio of the DW to the responsive growing period.

2.3. 3D virtual canopy reconstruction

Rice morphogenesis and plant architecture included measurement, specification and reconstruction using 3D architectural modeling

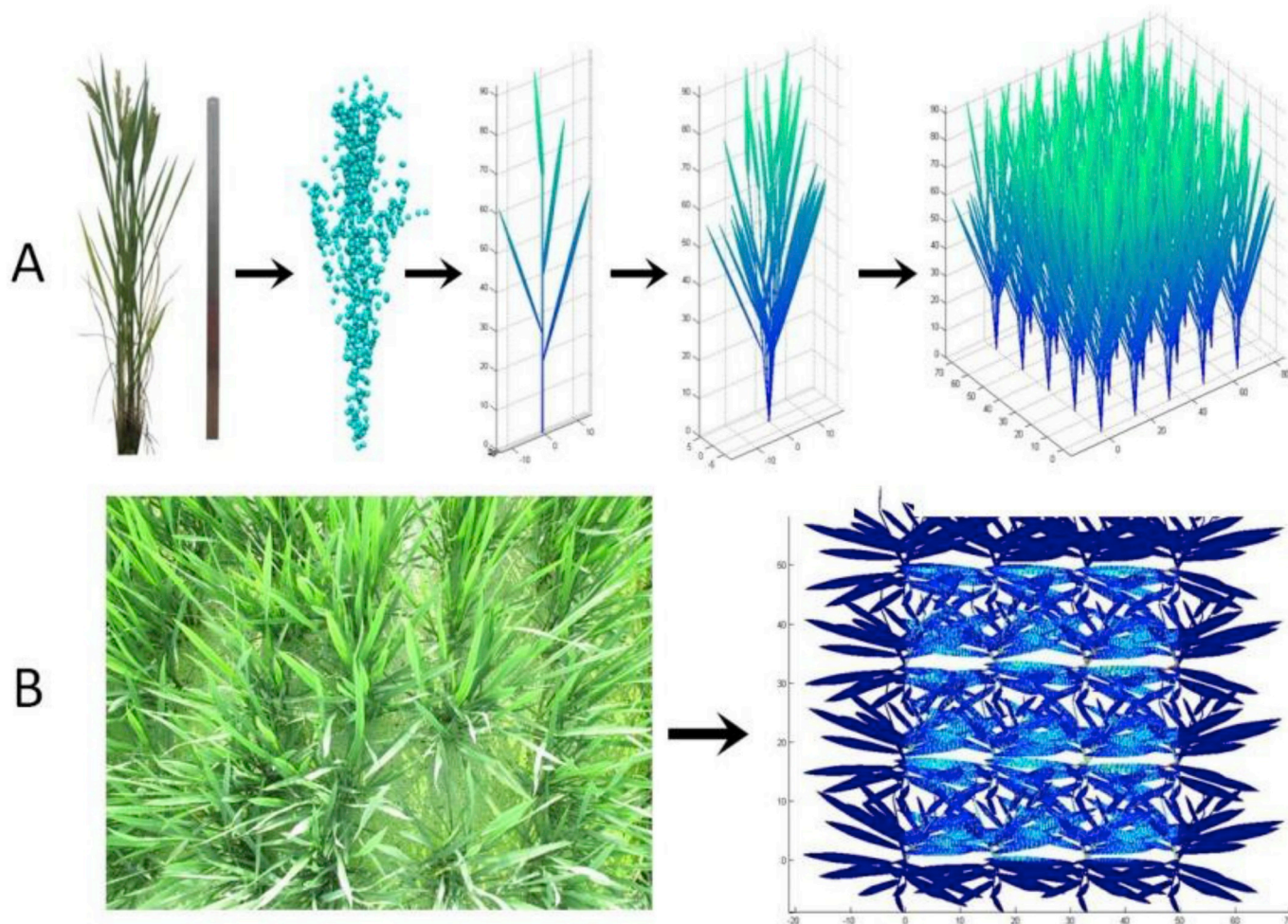


Fig. 1. Three-dimensional reconstructions of an individual rice plant (A) and rice community (B) based on the 3D digitized data.

(Fig. 1). The 3D coordinates of the rice plants were collected during the anthesis stage in the paddy field using an electromagnetic 3D digitizer (3Space Fastrak, Polhemus, Colchester, VT, USA). The 3D digitizer and method in our study were as accurate as that shown in previous studies (Wang et al., 2006; Zheng et al., 2008; Burgess et al., 2017), which were validated in our previous study (Li et al., 2012). The 3D coordinates of the rice plants were collected *in situ* in the paddy field using the 3D digitizer, and the topological information was recorded at the same time. Nine hills (three plants each in three rows) were digitized for the FP and SH treatments. A plastic film shed was built to minimize wind and rain disturbance during the digitizing and wooden boards were placed on the soil surface during these operations.

All the hills, tillers, stems, and leaves were separately numbered. Five to 20 points were digitized for each stem, the midrib of each leaf and the main axis of each panicle according to their length and curvature, with a maximum distance between successive points of 10 cm. One instrument of the 3D digitizer was used to distinguish and save the three-dimensional location of each digitized point. The digitized information for each stem and each leaf according to their corresponding hill and tiller number was manually saved (See Fig. 1. A).

In order to describe each stem and each leaf accurately with digitization, we digitized two times for each stem and three times for each leaf. For each stem, digitized points were taken from neck node with distance between successive points of 3–10 cm. And points were digitized on the opposite sides of stem. For each leaf, points were digitized from leaf tip with distance between successive points of 2–5 cm along the midrib. And then, points were digitized from leaf tip with distance between successive points of 2–5 cm along two leaf edges.

Each digitized plant was destructively sampled after field measurement. The measurements of the organ geometrical shape included the area, length, and maximum width of the blades using a portable laser area meter CI-203 (CID Inc., Camas, WA, USA); the length and the diameter of stems using a ruler and a micrometer, respectively; and the widths' equidistance along the blade midrib to describe the outline shape of the blades. With three people, it took 24 h to digitize 18 rice plants in the field and measure the organ geometry in the laboratory. There were approximately 3–6 wholly green blades and most of them had four blades at each stem. Measurements of tiller number, leaf number on the main stem, and plant height were conducted on 100 rice plants to determine the mean values for selecting a rice stand to digitize.

Canopy reconstruction and structural analysis were completed according to Zheng et al. (2008). The digitized points of the leaf midribs were interpolated using B-spline curves. A generalized quadratic equation was used to fit the normalized leaf width. The geometrical shape of a rice leaf was represented by triangular facets by connecting the interpolated points along the leaf midribs and margins. The stems and panicles were treated as a series of cylinders. Then, the 3D canopies of all of the digitized plots were reconstructed using a software Matlab 7.0 (MathWorks, Inc). The surface of each stem, leaf, and panicle was further divided into small facets, of which the maximum length of each side was 0.005 m and the corresponding spatial positions were characterized by their central points. Then, the area, inclination angle, and azimuth angle of each facet were calculated according to the 3D coordinates of the facet vertexes. The rice canopies were divided into horizontal layers at 0.02-m intervals. Leaf area distributions in the vertical profiles were characterized by leaf area density (leaf area per unit volume). The mean inclination angle distributions in the vertical profiles were characterized by summing the product of the angle and the area of the facets in each layer. The azimuth angle distributions were characterized by the ratio of the leaf area in every 10-degree class to the total leaf area. The vertical profiles of the cumulative leaf area (LA) and cumulative LAI of the FP and SH treatments at different altitudes in the anthesis stages were fitted using logistic models according to Dwyer and Stewart (1986).

2.4. Light measurements and analysis

Climatic data (daily solar radiation, minimum temperature, and maximum temperature) were collected from a weather station approximately 2 km from the experimental sites. A data logger (CR800, Campbell Scientific Inc., Logan, Utah, USA) was used as the measurement and control module. A silicon pyranometer (LI-200, LI-COR Inc., Lincoln, NE, USA) and temperature/RH probe (HMP45C, Vaisala Inc., Helsinki, Finland) were used to measure the total solar radiation and temperature, respectively. Daily solar radiation from transplanting to maturity was used to determine total accumulated solar energy. ϵ_i was measured between 1100 and 1300 h during the panicle initiation, anthesis, and maturity stages using a line ceptometer (AccuPAR LP-80, Decagon Devices Inc., Pullman, WA, USA). In each plot, light intensity inside the canopy was measured by placing a light bar in the middle of two rows and at approximately 5 cm above the water surface. Then, the light intensity was recorded above the canopy and ϵ_i was calculated as the percentage of light intercepted by the canopy [$100 \times (\text{light intensity above the canopy} - \text{light intensity below the canopy}) / \text{light intensity above the canopy}$] (Sinclair and Muchow, 1999). The integral of the intercepted solar radiation (S_i) during each growing period was calculated using the average ϵ_i and S_t during this growing period. S_i during the entire growing season (from transplanting to maturity) was the summation of S_i during the different growing periods. ϵ_c was calculated as the ratio of the aboveground DM to S_i (Plénet et al., 2000).

2.5. 3D light environment within a canopy

During the anthesis stage, light environment within a canopy were measured using a line ceptometer (AccuPAR LP-80, Decagon Devices Inc., Pullman, WA, USA). In the central district of each plot, the light intensity inside the canopy was measured along the rows (0, 10, 20, 30, 40, 50, 60, and 70 cm) and across the rows (0, 5, 10, 15, 20, 25, and 30 cm). All of the measurements were repeated at different altitudes from the ground (0, 20, 40, 60, 80, and 100 cm). A line transect was established at a given altitude using level rulers.

2.6. Nitrogen determination

N determination was completed during the panicle initiation, anthesis, and maturity stages. After DM measurement, different organs were oven-dried at 80 °C to a constant weight and separately ground using a mixer mill homogenizer (MM400, Retsch, Germany). Approximately 5.0 mg was used to determinate the N content per unit leaf area (N_L , g m⁻²), leaf N content (N_b , g m⁻²), filled grain N content (N_{grain} , g m⁻²), total aboveground N content (N_t , g m⁻²), postanthesis N content (Post- N_b , g m⁻²), and preanthesis N translocation per unit area of ground (N_{tr} , g m⁻²) using an NC analyzer (IsoPrime100 IRMS, Isoprime Ltd, UK). The N_{tr} was calculated by the following equation:

$$N_{tr} = N_{\text{grain}} - (\text{Post-}N_b) \quad (2)$$

2.7. Statistical analyses

One-way analysis of variance and multiple regression analysis were applied to assess the significance of the phenotypic responses using SAS 9.2 (SAS Institute Inc., USA). Critical correlations were tested using Pearson's correlation analysis. Means were tested using the least significant difference at the $P \pm 0.05$ level (LSD_{0.05}). Regression analyses between the parameters were performed using Sigma Plot 12 (SPSS Inc., Chicago, IL, USA). Regressions were fitted using linear and logistic models.

3. Results

3.1. Phenotypic plasticity of photosynthetic productivity

It is generally recognized that constraints in phenotyping capability resulting from ineffective crop management limit our capacity to interpret advances in high-yielding rice genotypes (i.e., super rice). In the current study, the grain yield of super rice was 8470 kg ha^{-1} in FP and 9930 kg ha^{-1} in SH (Wang et al., 2016a). The grain yield in SH was significantly higher than that in FP ($P < 0.05$), with 17.2% an increment compared to that in FP. The ϵ_i , S_i , LAD, CGR, and aboveground DM in SH were significantly improved compared to those in FP during the preanthesis, postanthesis, and whole growth stages, respectively (Table 1). The ϵ_c in SH was significantly higher than that in FP during the preanthesis and whole growth stages, but not during the postanthesis stage (Table 1). Generally, ϵ_i and S_i were positively and significantly correlated with total DM across practices and stages (Supplementary Fig. S1), while no significant relationship between ϵ_c and seasonal DM was observed (Supplementary Fig. S1). We argue that the high-yielding phenotype of super rice in SH improved light harvest and utilization, thereby leading to preminent photosynthetic performance and DM production (Table 1).

3.2. Alterations in canopy topology

The photosynthetic productivity for a given rice phenotype has relied extensively on phenotypic adaptation or plasticity in architectural and morphological topology because the distribution of leaf area and leaf inclination angle in a rice canopy determine the light interception and utilization and consequently influence final phenotypic productivity. For these reasons, the super rice morphogenesis and architecture including measurement, specification and reconstruction were developed during the anthesis stage in FP and SH using electromagnetic 3D visual modeling (Fig. 1). Apparent phenotypic alterations of super rice in architectural and morphological topology were found in a comparison between FP and SH, corroborating the fundamentality of agronomic manipulation for canopy topology (Fig. 2). Moreover, significant differences were found in the leaf area density distribution at four strata between FP and SH (Fig. 3). Super rice phenotype in SH provided a higher leaf area density at each stratum (Fig. 3).

3.3. Leaf dispersion

The vertical profiles of LA and LAI widely varied between two super rice phenotypes in FP and SH (Fig. 4). The super rice phenotype in SH had a notably larger LA and LAI at the middle parts of canopy (appr. 30–70 cm) than those in FP (Fig. 4A and B). The percentage of LA and LAI of the super rice phenotype in SH tended decrease in the upper parts of the canopy (appr. 60–90 cm), while it increased in the lower parts of the canopy (appr. 20–50 cm) in comparison to that in FP, respectively (Fig. 4C and D). Correspondingly, cumulative LA and cumulative LAI improved as altitude increased in both practices, of which in SH it grew more rapidly than that in FP (Fig. 5). The upward

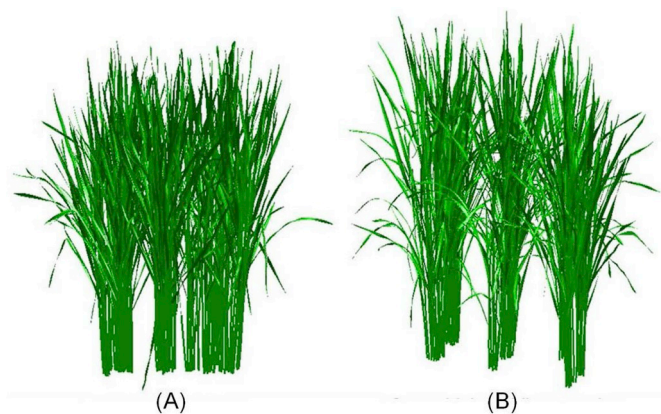


Fig. 2. Virtual rice images developed from the 3D representations of rice plant architecture during the anthesis stage. The canopies of the nine plants are shown for FP (A) and SH (B).

cumulative LA and LAI in the super rice phenotypes under SH were identically greater at different vertical altitudes than those in FP (Fig. 5). Logistic curve fit showed that the altitude of the peak of upward cumulative LA and LAI (h_0) in SH occurred earlier than that in FP, whereas the peak duration (Δh) between the two relative altitudes of inflexion (h_1 , h_2) showed limited variation between FP and SH (Fig. 5; Supplementary Table S2). Meanwhile, the maximum cumulative rate (V_m) and peak cumulation (GT) for LA and LAI during Δh were greater in SH than those in FP, respectively (Fig. 5; Supplementary Table S2). Super rice phenotypes in SH showed an improved cumulative rate and peaks of LA density than those in FP at the lower and middle parts of the canopies, further leading to a coincidentally increased LAI because of its high planting density (Figs. 3–5; Supplementary Table S2).

3.4. Leaf orientation

A proper distribution of leaf inclination angles is good for photosynthetic productivity, which in turn has profound effects on construction of “Ideotype” phenotypes. In our study, significant differences were found for the distributions of leaf inclination angles in the vertical profiles between the two practices (Figs. 6 and 7). The distribution for high leaf inclination angles (70–90°) in SH increased in comparison to that in FP (Fig. 6). Indeed, the increased distribution of high leaf inclination angles (70–90°) in SH primarily occurred in the upper canopy (Top 0–60 cm) (Fig. 7 A and B). There were very small phenotypic differences between FP and SH in terms of the leaf inclination angles and its distribution in the middle and lower parts of canopy (Top 60 cm–bottom) (Fig. 7 C and D). Generally, the leaves of the super rice phenotype in SH were more erect than those in FP across the whole canopy, particularly in the upper parts of the canopy (Top 0–60 cm) (Figs. 6 and 7). This implies that the super rice phenotype in SH had more erect foliage, allowing for more efficient light use.

Table 1

The efficiency of interception of solar radiation (ϵ_i), integral of intercepted solar radiation (S_i), leaf area duration (LAD), efficiency of conversion of intercepted radiation (ϵ_c), crop growth rate (CGR), total aboveground dry matter (DM) of FP and SH in pre- and post-anthesis stage, and during the whole stage.

Stage	Practice	ϵ_i (%)	S_i (MJ m ⁻²)	LAD (m ² d m ⁻²)	ϵ_c (g MJ ⁻¹)	CGR (g m ⁻² d ⁻¹)	DM (g m ⁻²)
Pre-anthesis	FP	63.7 ± 0.5 b	680.2 ± 5.7 b	253.8 ± 11.8b	1.57 ± 0.07 b	17.8 ± 0.7 b	1067.4 ± 39.9 b
	SH	65.6 ± 0.6 a	700.8 ± 6.9 a	286.1 ± 14.6a	1.76 ± 0.06 a	20.6 ± 0.8 a	1233.5 ± 47.2 a
Post-anthesis	FP	94.1 ± 0.2 b	439.0 ± 1.1 b	232.1 ± 5.4 b	1.29 ± 0.05 a	14.5 ± 0.5 b	566.9 ± 20.9 b
	SH	96.5 ± 0.3 a	547.8 ± 2.0 a	259.4 ± 12.9 a	1.40 ± 0.13 a	19.6 ± 1.9 a	766.2 ± 73.0 a
Whole	FP	72.9 ± 0.3 b	1119.2 ± 5.0 b	486.0 ± 13.5 b	1.46 ± 0.03 b	16.5 ± 0.3 b	1634.3 ± 27.7 b
	SH	76.4 ± 0.5 a	1248.6 ± 8.3 a	545.6 ± 26.7 a	1.60 ± 0.08 a	20.2 ± 1.2 a	1999.7 ± 114.9 a

Values are means ± SD. Values followed by the same letters indicate non-significance difference between FP and SH within stages at $P < 0.05$ (LSD test).

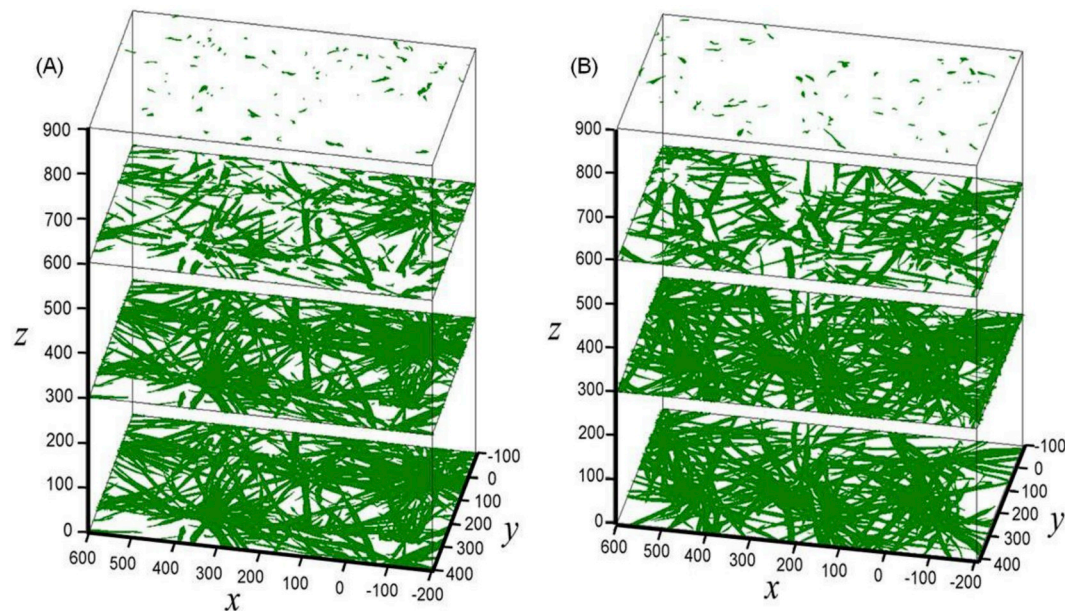


Fig. 3. Visualization of simulated leaf area density distribution for four strata in FP (A) and SH (B) during the anthesis stage, respectively. *x* represents the distance across rows (mm), *y* represents the distance along rows (mm), and *z* represents plant height (mm).

3.5. Light environment within a canopy

An “Ideotype” canopy would anatomically acclimate to an external light environment by dynamically modifying the photosynthetic light gradients. At a given position, the stem diameter and leaf length of the super rice phenotypes in SH were higher than those in FP, but the leaf

width and leaf shape were both nearly consistent between the practices (data not shown). Thus, the super rice phenotypes in SH showed a positive adaptation in foliage morphology. Given the aforementioned results, distinct differences were explored between the super rice phenotypes of the two practices in the distribution of light transmission under different altitudes along and across rows (Fig. 8). Meanwhile, the

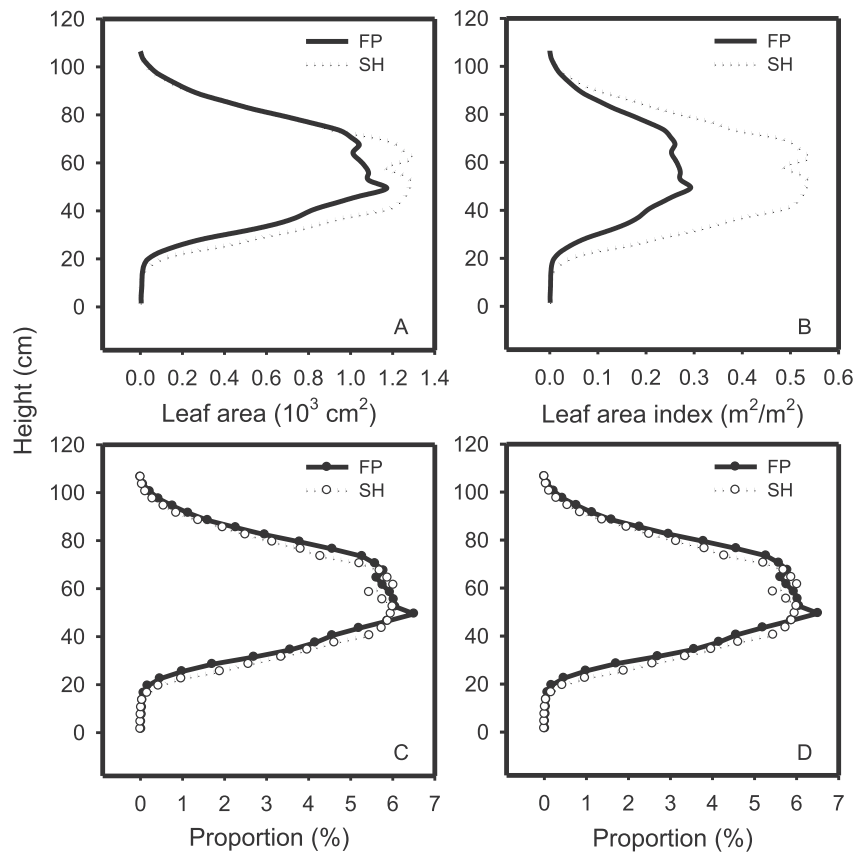


Fig. 4. Vertical profiles of leaf area (LA) (A) and leaf area index (LAI) (B), and the vertical proportion of LA (C) and LAI (D) in FP and SH at different heights during the anthesis stage.

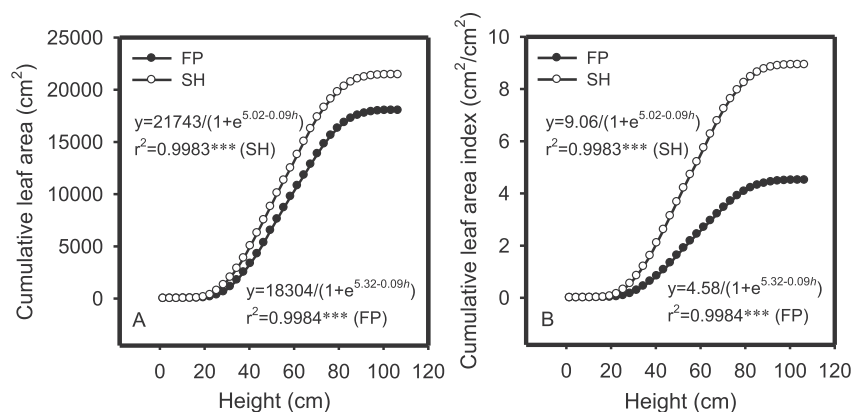


Fig. 5. Vertical profiles of cumulative leaf area (LA) (A) and cumulative leaf area index (LAI) (B) of FP and SH at different heights during the anthesis stage. Data were fitted using logistic simulation equations. Regression coefficients and significance are shown when $P < 0.05$ (***, $P < 0.001$).

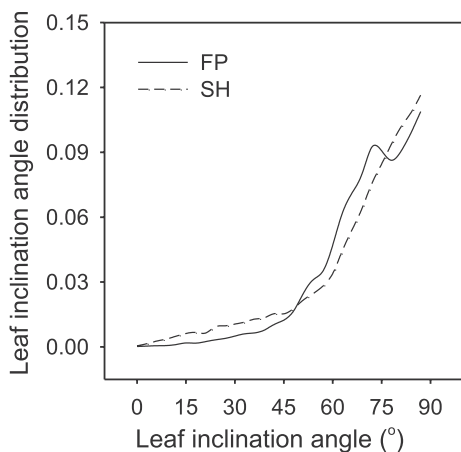


Fig. 6. Leaf inclination angle distribution across the rice canopy for FP and SH during the anthesis stage.

light transmission of the super rice phenotypes in FP gradually decreased from top to bottom (Fig. 8A and B), whereas the super rice phenotypes in SH showed a more abrupt reduction from the top to the middle part of the plants in comparison to FP (Fig. 8). In addition, the light intensity of the super rice phenotypes in SH was greater under different altitudes along and across rows in comparison to that of FP, in particular are lower than > 60 cm altitudes from the bottom to top (Fig. 8). Here, we demonstrate that the topological acclimation of super rice phenotypes in SH benefited from the light environment within a canopy.

3.6. Interaction of the nitrogen economy and photosynthetic performance

It is clear that leaf N economy is closely related to photosynthetic performance, since Rubisco accounts for a large fraction of leaf N. Our study further showed that N_t and SLN had significantly positive correlations with ϵ_c across practices and stages (Fig. 9). N_t was positively and significantly correlated with ϵ_b , S_b , and total DM across practices and stages (Fig. 10). This was supported by the results from the Pearson correlation analysis between N-related traits during the anthesis stage (N_b , SLN, N_t) and ϵ_b , ϵ_c , DM, and grain yield (data not shown). In addition, we found that the super rice phenotype in SH had a significantly improved preanthesis N_b , total N_b , N_{grain} , N_{tr} , N_{tr}/N_{grain} , and N_{tr}/DM_{grain} in comparison to that in FP (Table 2). This provides further evidence that the canopy photosynthetic productivity of a given rice phenotype is closely and positively related to leaf N content and canopy N accumulation. Stem number per hill during the early stage (Supplementary Fig. S2) and the leaf SPAD during the five key growth stages

(Supplementary Fig. S3) were also regarded as important physiological implications for high yield of super rice because of their positive responses to the N economy. Thus, the achieved high productivity of super rice in SH was the result of efficient phenotypic adaptation, which mainly featured the positive response of photosynthetic performance to the N economy.

4. Discussion

4.1. Phenotypic “reoptimization” of super rice for high yield

Progress has been made toward breaking the yield ceiling of irrigated rice by developing high-yielding phenotypes with optimized topological architecture. Chinese super rice emphasizes the top three leaves and the panicle position within a canopy and maximizes the source supply for grain filling, suggesting that an “Ideotype” approach is effective in breaking the yield ceiling of rice (Peng et al., 2008). As previously indicated, the evaluation of crop phenotypic plasticity based on variable architecture and morphology helps to dissect the genetics of quantitative traits related to yield. Improvement in high-throughput phenotyping has provided rapid and inexpensive genomic information (Araus and Cairns, 2014). However, the fact that ϵ_c had not been significantly improved with breeding progress could be concerning, particularly in light of reaching the theoretical limit of ϵ_p (Long et al., 2015). It is more likely that the canopy architecture and morphology of super rice needs to be “reoptimized” to enlighten further high-productivity breeding work.

In the current study, the super rice phenotype in SH achieved a significantly higher yield (17.2%) than that of FP. Most importantly, it approached the attainable yield potential based on our previous studies (Wang et al., 2016a, 2016b). The high-yielding super rice phenotype in SH had significantly improved ϵ_b , S_b , LAD, CGR, and DM during the preanthesis, postanthesis, and whole growth stages, and a significantly improved ϵ_c during the preanthesis and whole growth stages (Table 1). These points resulted in a high grain yield of super rice in SH. Furthermore, DM was significantly and positively correlated with ϵ_i and S_i rather than ϵ_c (Supplementary Fig. S1). This outcome also showed that there was some potential to improve ϵ_i and S_i by promoting “early vigor” (Rebolledo et al., 2015), introducing “stay-green” phenotypes (Thomas and Ougham, 2014) and the extending LA duration (Parry et al., 2011), while ϵ_c was penalized via canopy respiration because of the requirement to maintain LA (Murchie et al., 2009). We argue that the excellent ϵ_i and S_i performance of super rice phenotypes in SH primarily resulted from the reoptimized phenotypic topology (Figs. 2 and 3), finally making contributions to a high DM and grain productivity (Table 1). Thus, future progress in crop breeding requires a new emphasis on canopy light adaptation and harvest for specific, well-

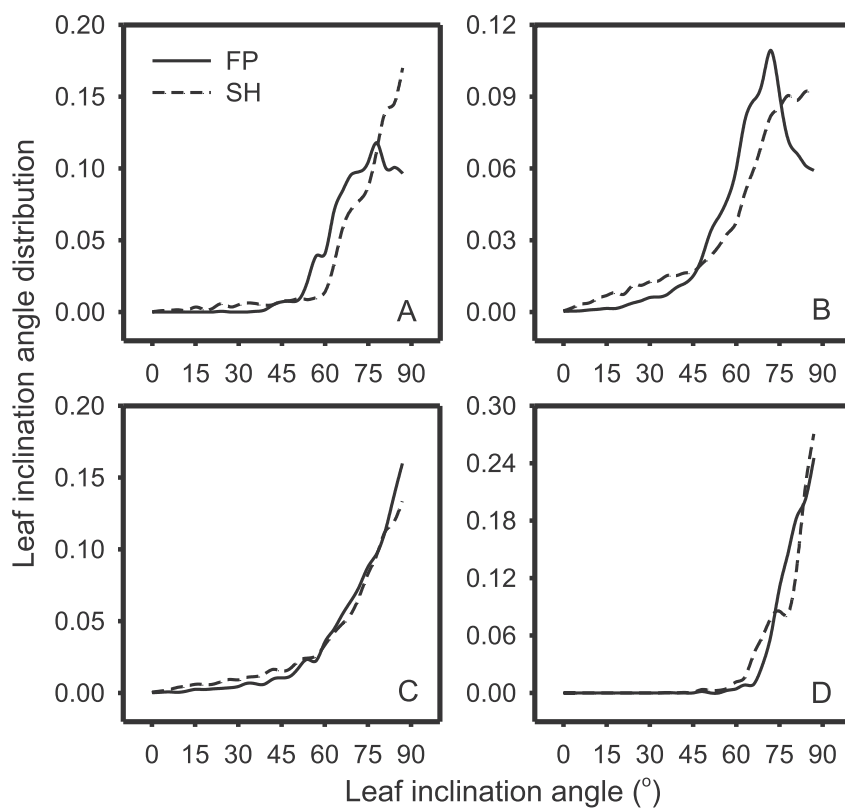


Fig. 7. Leaf inclination angle distribution in the rice canopy for FP and SH at four altitude intervals from top to bottom (Top 0–30 cm, A; Top 30–60 cm, B; Top 60–90 cm, C; Top 90–120 cm, D) during the anthesis stage.

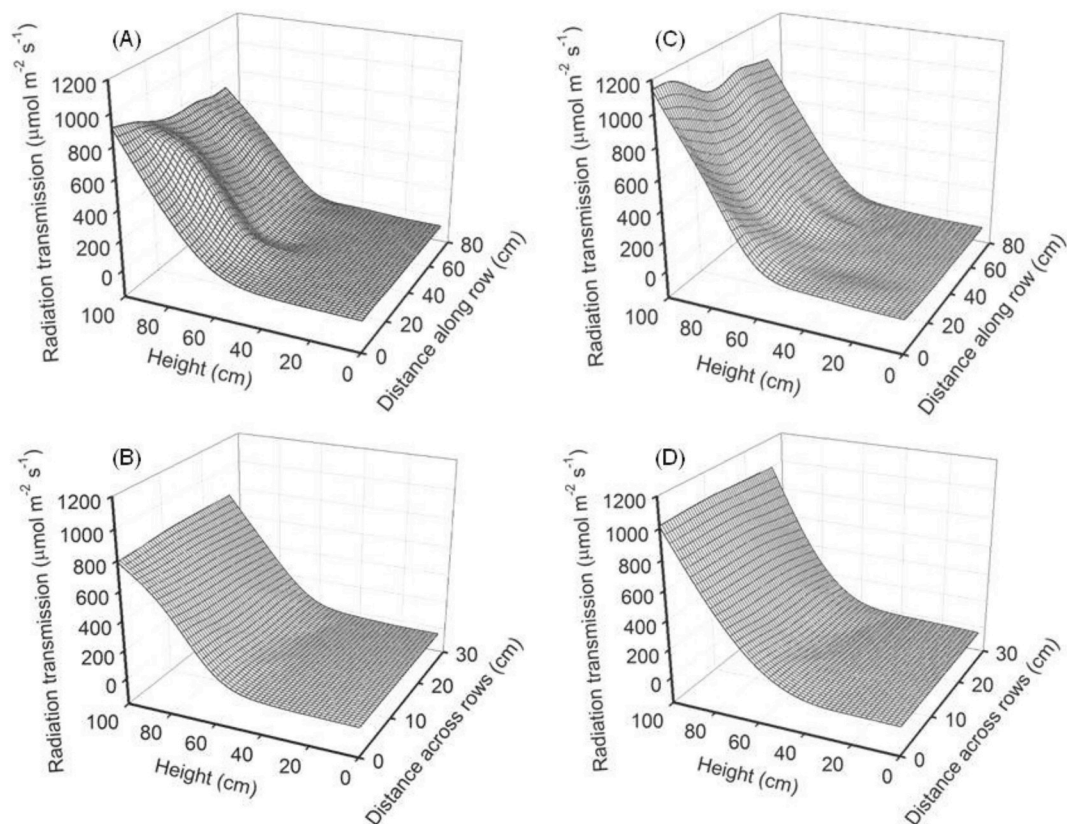


Fig. 8. Radiation transmission ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of FP (A, B), SH (C, D) under different heights along rows (A, C) and across rows (B, D) during the anthesis stage.

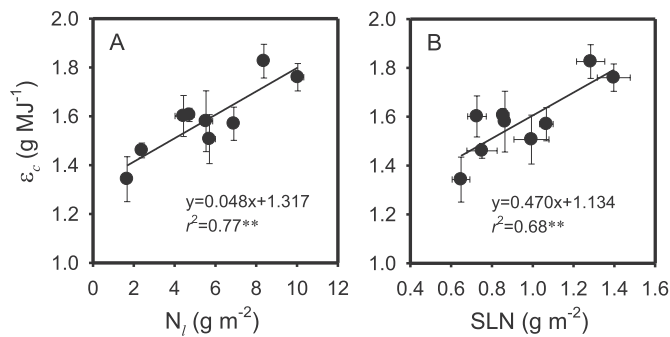


Fig. 9. Effect of leaf nitrogen content per unit area of ground (N_l) (A) and leaf nitrogen content per unit leaf area (SLN) (B) on the efficiency of intercepted radiation (ϵ_c) conversion. Values shown are mean $\pm$ SD. Data were fitted by linear adjustment. Regression coefficients and significance are shown when $P < 0.05$ (**, $P < 0.01$).

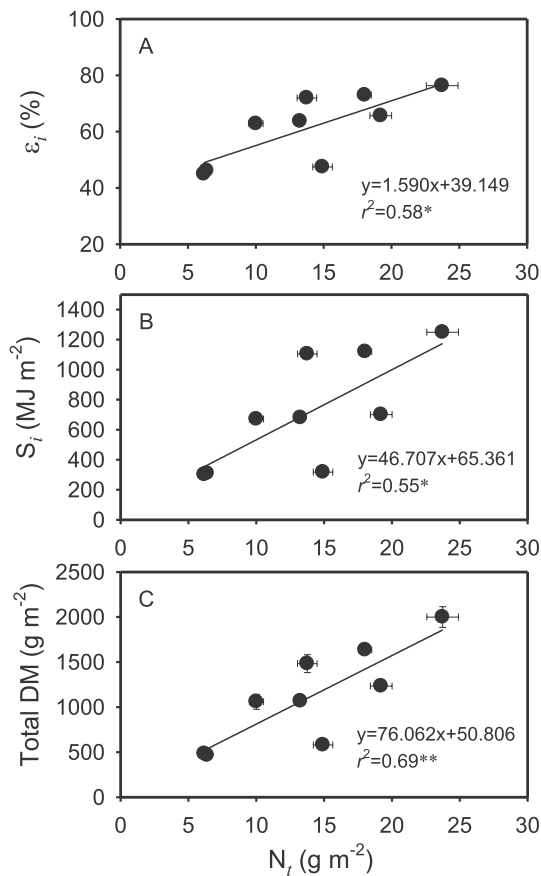


Fig. 10. Effect of total aboveground nitrogen content (N_t) on the efficiency of solar radiation (ϵ_i) interception (A), integral of intercepted solar radiation (S_i) (B), and total aboveground dry matter (Total DM) (C). Values shown are mean $\pm$ S. Data were fitted by linear adjustment. Regression coefficients and significance are shown when $P < 0.05$ (*, $P < 0.05$; **, $P < 0.01$).

defined traits of architectural topology. Future reoptimization of varietal character relies on integrated agronomic practice. It needs to increase plant N and K through proper nutrient management, and to increase plant density with optimal seedlings per hill.

4.2. Adaptation of light harvest to leaf dispersion and orientation

Canopy photosynthetic capacity depends on the acclimation of light-harvesting efficiency to growth irradiance (Evans and Poorter, 2001). In the present study, agronomic manipulations in phenotypic

Table 2

The pre-anthesis nitrogen content (Pre- N_t), post-anthesis nitrogen content (Post- N_t), total nitrogen content (Total- N_t), filled grain nitrogen content (N_{grain}), pre-anthesis nitrogen translocation per unit area of ground (N_{tr}), N_{tr}/N_{grain} , N_{tr}/DM_{grain} in FP and SH.

	FP	SH
Pre- N_t (g m ⁻²)	13.3 $\pm$ 0.3 b	19.2 $\pm$ 0.8 a
Post- N_t (g m ⁻²)	4.8 $\pm$ 0.4 a	4.5 $\pm$ 0.5 a
Total- N_t (g m ⁻²)	18.0 $\pm$ 0.5 b	23.7 $\pm$ 1.2 a
N_{grain} (g m ⁻²)	9.7 $\pm$ 0.2 b	11.5 $\pm$ 0.3 a
N_{tr} (g m ⁻²)	4.9 $\pm$ 0.2 b	6.9 $\pm$ 0.2 a
N_{tr}/N_{grain} (%)	50.7 $\pm$ 3.1 b	60.5 $\pm$ 3.6 a
N_{tr}/DM_{grain} (%)	0.64 $\pm$ 0.05b	0.80 $\pm$ 0.07a

Values are means $\pm$ SD. Values followed by the same letters indicate non-significance difference between FP and SH at $P < 0.05$ (LSD test).

architecture had significant effects on the photosynthetic productivity of the super rice (Figs. 2 and 3; Table 1). This was probably because leaf dispersion influenced the spatial distribution of the sunflecked LA, while leaf orientation influenced both the spatial distribution of the sunflecked LA and the distribution of the light transmission on leaf surfaces. Thus, developing optimal distributions of leaves to maximize light harvest and use efficiency has been a major approach for improving the productivity of rice (Long et al., 2006). Supporting previous work, this study also found that tillering plasticity affecting LA and dispersion was an important trait of plant architecture for grain yield (Supplementary Fig. S2). It is necessary to regulate the number of tillers for the maximum yield potential (Li et al., 2003). In addition, we proved that the LA distribution is an important determinant of light harvest in the canopy. Super rice phenotypes in SH provided a high cumulative rate and peaks of LA density (Figs. 3–5; Supplementary Table S2), leading to a coincidentally increased ϵ_i and S_i (Table 1).

Additionally, leaf orientation was identified as a key factor in determining both light utilization and the extent of photoinhibition (Murchie et al., 1999). In essence, super rice phenotypes in SH had more erect foliage, particularly in the upper parts of the canopy (Top 0–60 cm) (Figs. 6 and 7). Thus, that intercepted radiation was distributed over a higher proportion of the deployed leaf (Horton, 2000). More erect leaf angles are likely to reduce the proportion of leaves becoming photoinhibited (Werner et al., 2001; Falster and Westoby, 2003), thereby further contributing to a greater ϵ_c (Murchie et al., 2009). Similarly, genetic and molecular modification of rice architecture with erect leaves has been regarded as a feasible approach for improving rice grain yield (Li et al., 2009). However, yield superiority was not expressed because of the leaf erectness associated with a small leaf size results in a suboptimal LAI (Reynolds et al., 2000). As previously stated, it is likely that leaf vertical dispersion and the angular distribution of super rice need to be “reoptimized” through agronomic means to sustain profits in photosynthesis light harvest and use.

4.3. Adaptation of photosynthetic productivity to canopy light gradients

Light intensity within the canopy exponentially decreases with an increase in LA from the top to the bottom of the canopy (Hikosaka, 2014). Light capture is regulated by the amount and orientation of the leaves, and the duration during which a leaf is deployed. Light capture has a close relationship with photosynthetic productivity. Nevertheless, the aforementioned models of rice (Watanabe et al., 2005; Zheng et al., 2008) were unable to precisely predict the spatial and temporal heterogeneities of the light environment inside a defined canopy architecture. In the current study, we measured the light intensity at different altitudes inside the canopy using a line ceptometer (Fig. 8). Our study showed an active phenotypic acclimation in the canopy light gradients of super rice. Basically, super rice phenotypes in SH showed a more abrupt reduction from the top to the middle part of plants and

increased light transmission under different altitudes along and across rows in comparison to FP (Fig. 8). It is evident that these results were consistent with the phenotypic adaptation of light harvest to leaf vertical dispersion and angular distribution (Figs. 2–7). It has been believed that crop phenotypes with erect leaves permit more light transmission into the canopy with a relatively uniform radiation distribution (Setter et al., 1995). Given that solar radiation extinction coefficient decreases as leaf angle increases, we also agree that a low solar radiation extinction coefficient in the mid- and upper-canopy resulted in gradual light attenuation and deeper light penetration, particularly for a high LAI (Dickmann et al., 1990). Conclusively, erect foliage morphologies maximize the photosynthetic productivity per unit of light harvest by a leaf, and result in great photosynthetic performance in light utilization and DM production (Table 1).

4.4. Canopy photosynthetic performance in relation to nitrogen economy

Changes in photosynthetic capacity are driven by changes in both N_t and leaf N partitioning (Frak et al., 2001). In rice with a high supply of N, the light-saturated photosynthetic rate is correlated with the N_t and leaf Rubisco content (Li et al., 2009). Likewise, the potential activity of Rubisco and the capacity of chloroplastic electron transport are closely related to SLN (Gu et al., 2012). Correspondingly, our study further showed that N_t and SLN were significantly and positively correlated with ϵ_c (Fig. 9). N_t was positively and significantly correlated with ϵ_i , S_i , and total DM (Fig. 10). These points further support the results from the adaptation of photosynthetic productivity in SH to leaf dispersion and orientation and canopy light gradients (Figs. 2–10; Table 1). In light of the high N cost of leaf chlorophyll and chlorophyll-binding proteins, within-canopy alterations in ϵ_i depend on variations in N economy (Niinemets, 2007). Therefore, an improved N economy in SH made great contributions to the phenotypic “reoptimization” of super rice for high photosynthetic productivity.

On the whole, 3D visual modeling provided efficient evaluation of leaf area and orientation *in situ* in the paddy field. However, 3D visual modeling was a time-consuming manual work. Technically, the leaf shape was not considered in the studies of 3D visual modeling. 3D visual modeling was not effective to evaluate the influence of blade shape on canopy functioning in terms of potential photosynthesis.

5. Conclusions and implications

Our results show a promising perspective to increase phenotypic productivity of super rice via agronomic “reoptimization” of canopy topology. The “reoptimized” architecture of super rice in SH leads to major advances in leaf vertical dispersion and angular distribution in comparison to those in FP. These topological changes result in not only a higher cumulative rate and peaks of leaf density but also increased distribution of high leaf inclination angles in SH, particularly in the upper parts of the canopy. These points further sustain profits in photosynthetic acclimation to growth irradiance, N capture, and translocation, thereby leading to improved leaf area duration, light-harvesting capacity, light utilization, and photosynthetic efficiency for high crop productivity. The results presented here highlight the phenotypic “reoptimization” of super rice in leaf dispersion and orientation, light partitioning, and N economy.

The current study shows that large improvements in phenotypic productivity of super rice were achieved mostly by focusing on the adaptation of light harvest and use to leaf dispersion and orientation. The dependence between photosynthetic performance and N economy was necessarily a good indicator of yield promotion for super rice. Increasing leaf N should be viewed as a worthwhile aim in improving the photosynthetic capacity of super rice, and perhaps this should be separated from whether it could lead to an increase in N use efficiency. Admittedly, ϵ_i and N economy analysis, to some extent, are not sufficient to interpret the linkage between architectural “reoptimization”

and photosynthetic productivity at the canopy level. Further study should collect more detailed measurements of leaf photosynthesis and apply a canopy photosynthesis model to support these conclusions. Given that only one super rice genotype was examined, phenotypic plasticity of super rice across diverse genotypic backgrounds and agro-environments is needed. A larger frame will be placed upon how to balance the “reoptimized” canopy topology to increase canopy photosynthetic productivity, and more importantly, to enlighten higher-yielding super rice breeding work.

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CRediT authorship contribution statement

Depeng Wang: Formal analysis, Writing-Original Draft. **Shah Fahad:** Formal analysis, Writing-Original Draft, Writing-Review & Editing. **Shah Saud:** Writing-Review & Editing. **Muhammad Kamran:** Writing-Review & Editing. **Aziz Khan:** Writing-Review & Editing. **Mohammad Nauman Khan:** Writing-Review & Editing. **Hafiz Mohkum Hammad:** Writing-Review & Editing. **Wajid Nasim:** Writing-Review & Editing.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.plaphy.2018.11.010>.

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